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THE EFFECT OF VEGETATIVE COVER ON FORAGING STRATEGIES, HUNTING SUCCESS AND NESTING DISTRIBUTION OF AMERICAN KESTRELS IN CENTRAL MISSOURI

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ABSTRACT.—The hunting methods used by the American Kestrel (*Falco sparverius*) in relation to seven habitat types were studied in Boone County, Missouri, September 1981 through August 1984. Kestrels spent an average of 75% of each day hunting including 63% perch-hunting, 7% hover-hunting, 3.5% changing perch sites, and 1.5% in horizontal pursuit flight. Of 6359 kestrel foraging sites observed, use of disturbed grasslands was greater than expected (61%), use of croplands and woodlots was less than expected (3.5 and 4.0%), and use of old fields, undisturbed grasslands, and plowed fields was in proportion to availability. Kestrels cued on human-related disturbances in managed grassland habitat. There was no sex bias in use of habitat types by kestrels during any season. Kestrels were successful in 69.5% of their capture attempts and males were more successful than females. Invertebrates were captured most easily (82%), then rodents (66%) and birds (33%). Hunting success declined with increasing vegetation height. Hunting efficiency (estimated daily energy expenditures from time budgets and multiples of standard metabolic rate) was highest during perch-hunting. Time spent perch-hunting by kestrels decreased with increasing vegetation height. In capture/cost ratios, kestrels foraged most efficiently in disturbed grasslands, and least efficiently in old fields and croplands. Of 56 kestrel home ranges, 95% were in disturbed grassland habitat (which comprised 18% of the study area). These data suggest that the absence of suitable plant cover for kestrel foraging may effectively limit the distribution of American Kestrels in central Missouri.

Since the American Kestrel (*Falco sparverius*) is a relatively common and conspicuous raptor in Missouri (Toland 1984), inhabiting open areas and foraging along roadsides, farms and other habitats easily accessible to observers, it is a good subject for study of raptor foraging habitats. My objectives were to describe the hunting methods used by wild American Kestrels through an analysis of the relationship between vegetation height and density to foraging site selection, hunting strategy, hunting success, and nesting distribution of kestrels in central Missouri.

STUDY AREA AND METHODS

The study area comprised 175 km^2 in Boone County, Missouri and was composed mainly of farmland, woodlots, old fields, and meadows, and was interlaced by gravel roads. The area was divided into seven habitat types based on vegetation height, percent ground cover, and composition. Aerial photographs by the U.S. Geological Survey (1981), and ground reconnaissance were used in measuring percentages of different habitats. Vegetation height was measured to the nearest 2.5 cm and estimated visually for comparison until no difference between the two methods resulted. This was done every two wk and habitat availability was reassessed to provide monthly as well as annual means. I calculated mean habitat availability for the kestrel nesting period (March–August). Percent ground cover was estimated by sighting through an occular tube (four cm diameter/10 cm length; Weller 1956) pointed at the ground at arm's length. In each habitat type means from 20 readings were taken.

Croplands (wheat, corn, soybeans, etc.) made up 49% of the area. Lesser amounts of milo, oats, and tobacco were found in the study area. Three categories of croplands were recognized: 1) plowed fields, including light wheat stubble and newly planted winter wheat, 0–13 cm high comprising 25% of the study area; 2) crops, mainly wheat, corn, and soybeans 60–183 cm high, with an average ground cover of 90%, comprising 14% of the study area; 3) heavy, tall stubble 30–60 cm high, with an average ground cover of about 30%, comprising 10% of the area. Woodlots of 0.40–16.0 ha comprised 15% of the study area and had 75% ground cover. Important species included white oak (*Quercus alba*), black oak (*Quercus rubra*), hickory (*Carya* spp.), American elm (*Ulmus americana*), American sycamore (*Plantanus occidentalis*), black locust (*Robinia pseudoacacia*), honey locust (*Gleditsia triacanthos*), persimmon (*Diospros virginiana*), and Eastern red cedar (*Juniperus virginiana*). Old fields comprised 5% of the study area. Vegetation ranged 90–254 cm in height with 95% ground cover.

Grasslands comprised 31% of the area and were subdivided into two categories: 1) idle, undisturbed pastures and meadows 60–91 cm high, with an average ground cover of 90%, comprising 11% of the study area; and 2) disturbed grasslands (mowed, and grazed pastures and harvested hay fields) 5–25 cm high where ground cover was 90%, comprising 20% of the study area.

Actual habitat use by kestrels was compared with relative habitat occurrence. American Kestrels were observed in the field for three years from September 1981 through August 1984. During the first six mo, 36 kestrels were in the study area. During the next six mo (March–August 1982) I observed 13 territorial pairs. Between September 1982 and February 1983 an average of 48 birds was in

Table 1. Relative habitat use[a] by American Kestrels in central Missouri.

Habitat Type	Height (cm)	% Ground Cover	% Habitat Available	Habitat Use No.	Habitat Use %
Plowed fields, light stubble, newly planted crops	0–13	10	25 (11)	681 (295)	11.0 (9.0)
Disturbed grassland and fields (mowed, hayed, grazed)	5–25	90	20 (18)	3892 (2230)	61.0 (68.0)
Heavy, tall stubble fields	30–60	30	10 (7)	340 (131)	5.5 (4.0)
Idle, undisturbed pastures and meadows	60–91	95	11 (13)	660 (393)	10.5 (12.0)
Crops (corn, wheat, soybeans, milo, oats)	60–183	90	14 (31)	228 (98)	3.5 (3.0)
Old fields, overgrown pastures and meadows	90–254	95	5 (5)	291 (66)	4.5 (2.0)
Woodlots	>300	75	15 (15)	267 (66)	4.0 (2.0)
Total				6359 (3280)	100.0 (100.0)

[a] During nesting season in parentheses.

the 175 km^2 study area. During the period March–August 1984, 50 territorial birds (25 pairs) were present. Kestrels were captured with bal-chatri traps (Berger and Mueller 1959) or noose-harnessed House Sparrows (*Passer domesticus*; Toland 1985a), and then marked with painted U.S. Fish and Wildlife Service bands and colored plastic leg bands to facilitate individual recognition.

I used a 30x spotting scope and 9x binoculars to observe each kestrel. Each bird was observed a minimum of 20 min for a combined total of 1810 hr. I recorded type of activity (perch-hunting, hovering, soaring, preening, etc.), changes of perch, and duration (sec) of all flights. Type or types of vegetation within 50 m of a hunting kestrel, hunting method, capture success, type of prey (invertebrate, small mammal, or bird), and the sex of each foraging kestrel were recorded. When unable to see prey that kestrels unsuccessfully attempted to capture on the ground, I distinguished between invertebrates and small mammals by differences in strike characteristics. Wild American Kestrels attack ground-based invertebrates from a buoyant, parachuting strike and often hop or run after an insect if the initial pounce is unsuccessful. When attacking a small mammal, however, kestrels employ a dive or stoop without breaking their momentum until the last moment (pers. observ.). These differences in hunting techniques were reinforced by the performances of 12 falconry kestrels which I trained to hunt known prey types or "bagged" quarry during four yr (Toland, unpubl. data). All hunting attempts with undetermined outcomes were excluded from analysis. I distinguished between still-hunting from a perch and other perching activity by observation of associated behaviors such as head-bobbing, sleek plumage with frequent plumage rousals (shaking), and erect, alert posture. Observations of kestrels were made during all daylight hr including as many full days as possible. Otherwise, half-day observations were alternated in mornings and afternoons.

Birds were located by driving secondary roads. A census route of about 120 km was driven at an average speed of 40 km/hr. An average lateral distance of 800 m each side of the route was effectively covered by two observers. The area was intersected by a network of roads every 1.6 km, thus the route allowed complete surveillance of the study area. At least one census/wk was completed during three yr. Censuses were conducted between 1000 and 1400 H on days with conditions of good visibility and low wind velocity. All kestrel sites were plotted on cover maps during each of the three nesting seasons.

I estimated daily energy expenditures using observed time budgets and multiples of standard (basal) metabolic rate (SMR) (Koplin et al. 1980; King 1984) to determine differences in daily energy budgets (DEB) due to different hunting methods in vegetation of various heights. A multiple of 1.7 × SMR has been used for resting metabolic rate (RMR) (Wolf and Hainsworth 1971). This is the rate of diurnal inactive metabolism and includes SMR as well as heat liberated in thermoregulation and digestion (Gessaman 1973). Therefore, I used 1.7 as the value of the energetic cost of inactive perching and loafing. I used 1.0 as an index to the energetic cost of nocturnal inactivity (Gessaman 1973). I estimated cost of preening, stretching, eating, caching, and other maintenance activity as 2.0 × SMR. I used a multiple of 3.5 × SMR for still-hunting from a perch (Wakeley 1978b). I used 8.0 as an index to the cost of changing perching spots (Tucker 1971; Wakeley 1978b). Energy consumption during fast forward flight used in pursuit has been estimated at 12.5 × SMR (Wakeley 1978b; Rudolph 1982). Therefore, I used 12.5 as an index to the cost of swift horizontal chases as well as hovering—kestrels compensate for the lift lost by lack of forward velocity by fanning the tail and utilizing wind and surface updrafts (Tucker 1968; Rudolph 1982). I converted prey capture rates to estimates of the number of captures/unit cost by dividing each rate by its respective energy : cost index (Wakeley 1978b). A comparison was made between these capture : cost ratios and amount of time kestrels used each hunting method and each type of habitat.

RESULTS AND DISCUSSION

During the average 10 hr period of daylight, American Kestrels spent an average 75% of their time hunting and 25% loafing, eating and caching, and preening and stretching. Average daily activity of kestrels included 63% still-hunting, 3.5% directional change of perch, 7.0% hovering and 1.5% horizontal pursuit or tail-chasing.

Foraging Site Selection. I observed foraging kestrels 2131 times during the first yr, 2363 the second yr, and 1865 the third yr. The distribution of sites selected were not significantly different among the three yrs, so data were combined (Table 1).

Kestrels hunted over disturbed grasslands 61% of the time or three times the frequency with which this habitat occurred in the study area ($\chi^2 = 84.05$, $P < 0.01$, df = 6; Table 1). By the same measure, kestrels significantly under-utilized crops and woodlots ($\chi^2 = 61.6$, $P < 0.01$, df = 5; Table 1). Undisturbed grasslands, old fields and plowed fields were used in proportion to availability ($\chi^2 = 1.67$, $P > 0.05$, df = 2).

During the nesting season (March–August) habitat availability changed substantially, croplands increasing from 14% to 31%. Kestrels exhibited even stronger preference for disturbed grassland during this season, conducting 68% of their foraging in this habitat (Table 1). During the nesting season, kestrels hunted in disturbed grassland more than expected and in crops and woods significantly less than expected ($\chi^2 = 177.8$, $P < 0.01$, df = 6). Kestrel use of available old fields, undisturbed grasslands, and plowed fields did not deviate significantly from expected values ($\chi^2 = 3.52$, $P > 0.05$, df = 2).

Kestrels were probably attracted to disturbed grassland, since 1) low vegetation in pastures and fields afforded good visibility of small mammals, 2) shorter, flexible grasses would give little resistance to the strike of the light-weight kestrel, and 3) disturbances by farm workers, machinery and livestock would increase movement and thus vulnerability of small mammals. Shrubb (1980) reported similar behavior by the Eurasian Kestrel (*Falco tinnunculus*), which made 62% of their kills in uncultivated grasslands, roadsides, and field edges comprising 24% of a study area in England. Shrubb also reported that Eurasian Kestrels avoided cereal crops during the nesting season. His opinion was that the combination of height, density, and evenness of cereal crops inhibited successful searching, and the stiff, dense, spikey nature of the plants made prey capture difficult. A preference for haylands and pastures with good interspersion and avoidance of large tracts of cropland has also been reported for the Ferruginous Hawk (*Buteo regalis*) (Wakeley 1978a, 1978b; Gilmer and Stewart 1983), the Swainson's Hawk (*B. swainsoni*) (Bechard 1982), the Red-tailed Hawk (*B. jamaicensis*), and the Rough-legged Hawk (*B. lagopus*) (Baker and Brooks 1981). Craighead and Craighead (1956) reported higher buteo densities in habitats with shorter vegetation and sparser ground cover even though vole populations were lower.

When choosing hunting sites, kestrels in my study area were quick to cue on recently harvested crop and hay fields as well as other human-related disturbances such as plowing and mowing. These disturbances result in sudden decreases of cover and increases in rodent vulnerability. Kestrels responded so consistently to these disturbances that I was able to predict their foraging sites on the basis of farming activities. Kestrels also cue on other human-caused disturbances, such as irrigation in California (Rudolph 1982) and controlled fires in Florida (Smallwood et al. 1982). Kestrels in central Missouri commonly hunted in and around herds of livestock, apparently finding voles (*Microtus* spp.) highly conspicuous when flushed by foraging sheep, cattle or horses. Usually kestrels hovered 4–10 m above sheep but sometimes flew quickly over, around, and under grazing cattle. Shrubb (1980, 1982) found that Eurasian Kestrels in England also responded to habitat disturbances. Bechard (1982) found nesting Swainson's Hawks avoided cropland before harvest and concentrated on pastures and edge with less cover, although good concentrations of rodents were present in wheat fields. However, when harvest reduced cover, fields were extensively hunted by the hawks.

Differential use of winter habitats by both sexes has been reported for kestrels in Texas, California, Arizona, Mexico (Koplin 1973; Mills 1976), and

Georgia (Stinson et al. 1981), but was not found in Kentucky (Sferra 1984) nor in my area ($\chi^2 = 10.77$, $P > 0.05$, df = 6).

Hunting Success. Kestrels were successful in 988 of 1414 (69.5%) capture attempts during the three yr. Hunting success was higher during the nesting period (March–June) than in winter (November–February) though the difference was not statistically significant ($\chi^2 = 3.72$, $P > 0.05$, df = 1). Higher hunting success during nesting probably reflects greater prey abundance and/or vulnerability during the spring. Males were more successful hunters (72%) than females (67%) year-round ($\chi^2 = 3.98$, $P < 0.05$, df = 1), but there was no difference in hunting success of males and females during winter ($\chi^2 = 0.014$, $P > 0.05$, df = 1). Better hunting success by males may be an adaptation by which males provide food for both females and nestlings during much of the nesting period (Cade 1982; Toland 1986), or greater prey abundance and vulnerability during the nesting cycle when males are primary foragers may affect their higher success rates.

Kestrels in my study area had an 82% success rate in capturing invertebrates, 66% success in capturing rodents and 33% success in capturing birds ($\chi^2 = 127.08$, $P < 0.01$, df = 2) (Toland 1983, 1986). During the nesting season, the overall capture rate increased to 74% of 580 attempts even though the percentage of vertebrate prey increased to 81.5% (Toland 1983). Kestrels became more aggressive and rapacious during the nesting season when it was probably more energy efficient to capture larger vertebrate prey than invertebrate prey when raising broods (Cade 1982). To investigate this phenomenon I offered handicapped European Starlings (*Sturnus vulgaris*) to kestrels during both nesting and non-nesting seasons. Although attracted to within a few m of 16 starlings offered, kestrels did not attempt to kill them during the non-nesting period. However, during the nesting season, kestrels killed 12 of 16 starlings ($\chi^2 = 21.87$, $P < 0.01$, df = 1).

The overall hunting success of kestrels in my study was higher than previously reported elsewhere, perhaps due to a high density of Prairie Voles (*Microtus ochrogaster*). Voles were so abundant that they could be seen frequently in all habitats. Interviews with farmers in my study area supported this qualitative assessment. The high hunting success rate of kestrels in central Missouri is even more significant when considering that vertebrates (mainly voles) comprised 67% of the prey captured. Balgooyen (1976) found a similar proportion of vertebrate prey (70%) in kestrel diets in California. However, most studies report higher percentages of invertebrates than vertebrates, including Jenkins (1970; 39% success, 33% vertebrates) in Costa Rica, Sparrowe (1972; 33% success, 21% vertebrates) in Michigan, Cruz (1976; 42% success, 39% vertebrates) in Puerto Rico, Collopy (1979; 55% success, 6% vertebrates) in California and Rudolph (1982; 57% success, 5% vertebrates) in California.

Height and density of vegetation in kestrel ranges had a considerable effect upon their hunting success (Table 2). With the exception of plowed fields where kestrels hunted mostly for insects and earthworms, hunting success declined significantly with increasing vegetation height ($\chi^2 = 182.14$, $P < 0.01$, df = 6). The greatest number of hunting attempts (705) and captures (83%) were made in managed or disturbed grassland (5–25 cm high), while only 41% of 79 attempts were successful in crops and woodland.

Hunting Efficiency. Kestrels use three distinct hunting methods which vary in efficiency and energetic cost (Rudolph 1982). Kestrels still-hunt from an elevated perch 70–97% of the time (Cruz 1976; Balgooyen 1976; Cade 1982; Rudolph 1982). Kestrels hunt from a hover 2–20% of the time (Balgooyen 1976; Rudolph 1982), and in swift, horizontal flight <5% of the time. Kestrels in my study still-hunted from a perch 88% of the time and from a hover 10% of the time, while swift, horizontal flights to include tail-chasing and contour-hugging were used 2% of the time (Table 2). Vegetation height apparently influenced the hunting strategy used by kestrels. Time spent still-hunting declined with increasing height of vegetation while time spent hovering significantly increased ($\chi^2 = 50.74$, $P < 0.05$, df = 6; Table 2). Since hunting methods differ in energetic costs and kestrels use them in proportions varying with the vegetation at foraging sites, vegetative structure probably influenced the ability of kestrels to maximize energy gain.

Kestrels were successful in 76% of hunting attempts from perches (Table 3), which was significantly higher than success from hover-hunting (52%) ($\chi^2 = 55.15$, $P < 0.001$, df = 1) or horizontal flights (45%) ($\chi^2 = 48.2$, $P < 0.001$, df = 1). I calculated capture/cost values of 22.0, 4.7, and 3.7 for still-hunting, hovering, and horizontal pursuit, respectively. The average use of these hunting methods by kestrels was roughly proportional to their respective

Table 2. Hunting strategies and success of American Kestrels foraging in seven habitat types in central Missouri.

Habitat Type	Height (cm)	% Ground Cover	% Hunting Strategies Used: Perch-Hunting	Hovering	Flapping Flight	Hunting Success: Captures/Attempts	% Success
Plowed fields, light stubble, newly planted crops	0–13	10	92	7	1	67/91	74
Disturbed grassland and fields (mowed, hayed, grazed)	5–25	90	91	8	1	583/705	83
Heavy, tall stubble fields	30–60	30	81	18	1	79/122	65
Idle, undisturbed pastures and meadows	60–91	95	72	27	1	92/175	53
Crops (corn, wheat, beans, milo, oats)	60–183	90	68	30	2	28/67	42
Old fields, overgrown pastures and meadows	90–254	95	68	30	2	35/106	33
Woodlots	>300	75	92	6	2	4/12	33
Means	—	—	88	10	2	—	—
Totals	—	—	—	—	—	888/1278	69.5

capture/cost ratios. Thus, kestrels used the most efficient method (perch-hunting) most often, as previously reported by Sparrowe (1972), Collopy (1979) and Shrubb (1982). Perch-hunting was used 91% of the time in disturbed grasslands where kestrels foraged 61% of the time with a success rate of 83%. Kestrels perch-hunted only 68% of the time in cropland and old fields and hunted only four and 6% of the time, respectively, in these two habitat types; capture success rates were 42 and 33%, respectively.

I estimated an average daily energy budget of about 60 kcal, although this value could vary with daily temp or season, and body weight of the birds (Koplin et al. 1980). During the nesting season, when adults in central Missouri are usually feeding five nestlings (Toland 1985b), it becomes increasingly obvious why kestrels hunt in habitat where they can forage most efficiently. Of 56 nesting season home ranges, 95% (all but three) were in disturbed grassland habitat. Thus, most of the nesting kestrels in my study area were concentrated in 18% of the available habitat. As vegetation increases in height, detection and capture of prey become more difficult. Because the prey animal is vulnerable to predation only for brief moments, kestrels foraging in these habitats must depend on hunting methods which afford close proximity to prey. These methods include hovering and horizontal flight during contour-hugging or tail-chasing, and are energetically at least four times more costly than perch-hunting, which may explain why kestrels spend so much time foraging in habitat where they mostly still-hunt from perches.

The importance of habitat physiography is com-

Table 3. Success of American Kestrel hunting strategies 1981–83.

Sex	Still-hunt: Captures/Attempts	%	Hover: Captures/Attempts	%	Tail-chase: Captures/Attempts	%
Males	478/611	78	80/141	57	34/69	49
Females	333/451	74	48/103	47	15/39	38
Total	811/1062	76	128/244	52	49/108	45

pounded during the nesting season when adult American Kestrels must provision five or six nestlings whose daily energy requirements exceed adults (Cade 1982). This critical time period demands that kestrels forage as efficiently as possible, and could explain why 95% of the nesting pairs had home ranges composed of disturbed grasslands. The scarcity of suitable plant cover effectively limits the distribution of American Kestrels in central Missouri and may explain declines of several species of hawks in areas where expansive monoculture farms predominate.

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Research/Teaching Assistantship Wanted. Serious raptor student seeking M.Sc. research/teaching assistantship to begin Fall 1987. Interested in virtually any aspect of raptor ecology or behavior, especially raptor–prey ecology, habitat requirements, and population modeling. Willing to consider almost any locality, but prefer western U.S. or Mexico. Have B.S. in Wildlife Science, published research, and a variety of experience. GRE scores, transcripts, recommendations, etc., available. **Please contact: Bryan Kimsey, P.O. Box 278, Anahuac, TX 77514, (409) 267-6527.**

Newly-Appointed Vice President of the Society for the Preservation of Birds of Prey. The Reverend Edward D. McGinnis of Elizabeth City, North Carolina, was named Vice President of the Society for the Preservation of Birds of Prey on 29 December 1986. Reverend McGinnis was born in Durham, North Carolina, and received his B.A. degree in religion and philosophy from Elon College in 1969. **He can be contacted at P.O. Box 2448, Elizabeth City, NC 27909.**